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RESPIRATION IN SOME ATLANTIC REEF CORALS IN RELATION TO VERTICAL DISTRIBUTION AND GROWTH FORM

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The rates of respiration of lower animals are determined, to a large extent, by a series of phenotypic adaptations or acclimations to specific factors in their environments. The integrated effects of these can be observed by comparing the rates of respiration of animals from habitats which are subject to different combinations of environmental factors (Davies, 1967). In hermatypic corals, those colonies living at greater depths on the reef experience both qualitative and quanitative differences in light regime. This in turn results in considerably lower rates of photosynthetic carbon fixation by the zooxanthellae in the coral tissues (Davies, 1977). Since it is now clear that a significant part of the fixed carbon is translocated to the coral tissues (Muscatine, 1973), it is possible that the overall nutritional input is lower in corals living at greater depths. Since respiration rate may be determined by the level of food intake (Davies, 1967), this study was undertaken to investigate possible intraspecific differences in the rates of respiration of corals, associated with habitat depth, and also to compare the rates of respiration of corals of different growth forms.

Although a number of earlier studies have presented data on the rates of respiration of corals (e.g. Yonge, Yonge and Nicholls, 1932; Kawaguti, 1937; Franzisket, 1969), comparisons of rates between different specimens of coral were not possible since the quantities of coral tissue involved were not measured. Ideally, respiration rates should be expressed on a unit basis which relates to the mass of respiring tissue, and which is not itself subject to change with the environmental factors being studied. In this paper, respiration rates are expressed in terms of the dry weight of the respiring coral tissue (including its contained zooxanthellae). Values are also given in terms of the surface area of the colony occupied by coral tissue since this is of particular value in studies on the primary productivity of corals. All experiments were carried out at the Discovery Bay Marine Laboratory, Jamaica.

Materials and Methods

The following species were examined: *Montastrea annularis* (massive growth form) depth 3 to 40 m; *M. cavernosa* (massive), depth 13 to 80 m; *Acropora palmata* (branching), depth 5 m; *A. cervicornis* (branching), depth 15 m; *Agaricia lamarcki* (plate-like), depth 40 m; *A. undata* (plate-like), depth 65 m; *A. grahamae* (plate-like), depth 80 m. Coral heads of about 5 cm diameter were collected using SCUBA, with the exception of those from depths of 65 and 80 m which were collected by a NEKTON submersible (General Oceanographics Inc.). The corals were brought ashore in buckets of sea water and transferred to a running seawater aquarium without exposing the animals to the air. Any corals which were found

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to have an endozoic or burrowing fauna were rejected. Regrettably, all of the specimens of *Montastrea cavernosa* collected from 80 m were completely riddled with boring sponges, which invalidated any attempts at measuring their rates of respiration. The corals were kept overnight before use and inspected to ensure that the polyps expanded naturally and there was no apparent tissue damage.

Rates of oxygen consumption were measured polarographically with a Beckman 221 oxygen electrode, inserted into a closed plexiglass chamber. The chamber, which had a volume of 253 ml, had a magnetic stirrer in the base and was surrounded by a water jacket maintained at 28° C. All measurements were carried out in darkness by covering the chamber with opaque black PVC sheet. The rates of respiration, which were not affected by the drop in oxygen partial pressure down to 50% of saturation, were derived from a linear pen-recorder trace. The duration of a single run was never more than 30 min.

At the end of the experiment, the volume of the coral was determined by measuring the volume of water in the chamber and subtracting from the volume of the chamber. The surface area occupied by living coral tissue was then measured by cutting and shaping aluminum foil to the coral head and then weighing the foil (Marsh, 1970; Johannes and Tepley, 1974). The head was then fixed in 10% formaldehyde for 24 hr before being decalcified in 10% HCl. (Future use of formaldehyde in this technique is not recommended because of the possibility of the formation of carcinogenic Bis-chloromethyl ether.) This procedure left an intact sheet of fixed coral tissue, from which the tufts of boring filamentous algae could be lifted. The tissue was then dried at 105° C for 24 hr.

In order to make an estimate of the loss of tissue material as a result of the fixation and acid treatment, a check was subsequently carried out using the British sea anemone *Actina equina*. Each anemone was divided into three pieces by means of radial cuts, and blotted to superficial dryness on filter paper. The first piece was weighed and then dried at 105° C, the second piece was weighed, immersed in 10% formalin for 24 hr and then dried and the third piece had an additional 24 hr in 10% HCl. Using six replicates it was found that the mean dry weight of the untreated piece was 19.0% of the fresh weight. The formalin treatment resulted in a mean loss of 9.2% of the dry weight and the formalin and acid treatment resulted in a further loss of 2.0%. It must therefore be borne in mind that the values for dry weights of coral tissue may be about 10% too low and that the unit-weight respiration rates would therefore be about 11% too high.

Results

Intra- and interspecific variations with depth

Specimens of *Montastrea annularis* were examined from water depths of 2, 10, 20 and 40 m. From Figure 1 and Table I it can be seen that the rate of weight-specific oxygen consumption decreases progressively with increase in depth, so that the respiration of the deepest corals is less than half of that of the shallow-water forms. The greatest difference is observed in the relatively small depth change between the shallow-water colonies living at 2 m when compared with those living at 10 m.

Similarly, a change is noted when comparing specimens of *Montastrea cavernosa* from 13 m (the shallowest depth at which it occurred) with specimens living at

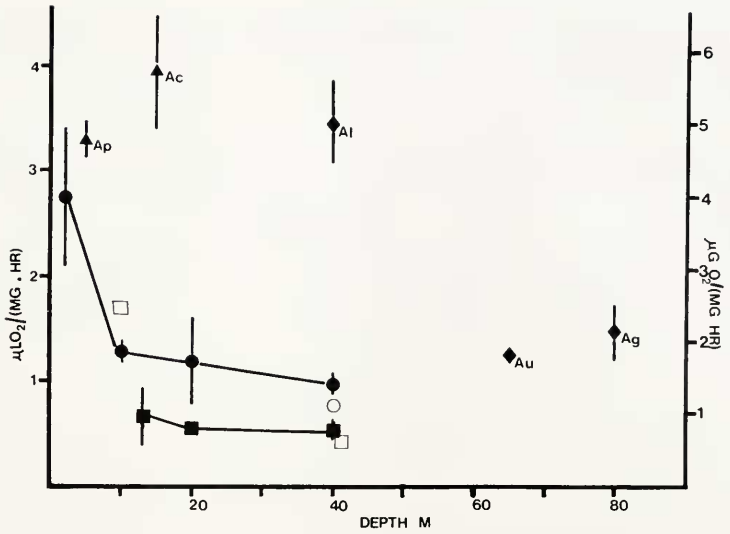

FIGURE 1. Weight-specific respiration rate of corals plotted against the depth at which the animals were living. Solid triangle, *Acropora:*—Ap *Acropora palmata;* Ac *Acropora cervicornis;* solid diamond, *Agaricia*—Al *Agaricia lamarcki;* Au *Agaricia undata;* Ag *Agaricia grahamae;* solid circle, *Montastrea annularis;* solid square, *Montastrea cavernosa.* The two open symbols represent specimens transplanted from shallow to deep water and *vice versa.* Vertical bars indicate standard deviations.

20 m and 40 m. The decrease in rate of respiration with increase in depth is also evident when surface-area-related respiration rate is plotted (Fig. 2).

Most other Caribbean corals exhibit a much more restricted depth-distribution range, rendering intraspecific comparisons impossible. However, it is possible to make interspecific comparisons among species of *Agaricia* with very similar growth forms, but with differing depth distributions. Again from Figures 1 and 2 it can be seen that specimens of *Agaricia lamarcki* from 40 m have markedly higher rates of respiration than those of *A. undata* from 65 m or of *A. grahamae* from 80 m.

In order to test whether the intraspecific differences in respiration rates are phenotypic responses to the particular environment at that depth, reciprocal transplantation experiments were carried out. Specimens of *M. cavernosa* and *M. annularis* from 40 m were transplanted to a depth of 10 m and *vice versa.* After 5 weeks they were removed from the reef, and their respiration rates measured. It was noted in both species that the 40-m specimens transplanted to 10 m had expelled most of their zooxanthellae but the corals nevertheless were apparently in good condition. The shallow corals transplanted to 40 m showed no apparent change. Regrettably, because of logistic difficulties, respiration-rate values are only available for one specimen from each transplantation site and the specimens of deep-water *M. annularis* transplanted to 10 m were lost. Figure 1 shows that in both species the rates of respiration had changed in the 5 weeks following transplantation: those transplanted to deep water had lowered their respiration rates, and *vice versa.* This suggests that in those species with a wide depth-distribution range, the depth-related respiration rate may be a phenotypic response to environmental factors.

TABLE 1

Respiration rates of corals, expressed on a unit basis of mg dry weight of tissue and surface area of living tissues ± standard deviations.

	n	Respiration rate			n	Respiration rate	
		$\mu l\ O_2/(mg \cdot hr)$	$\mu l\ O_2/(cm^2 \cdot hr)$			$\mu l\ O_2/(mg \cdot hr)$	$\mu l\ O_2/(cm^2 \cdot hr)$
Montastrea annularis				*Montastrea cavernosa*			
2 m	3	2.75±0.7	18.05±7.2	13 m	3	0.78±0.26	9.21±1.8
10 m	4	1.27±0.06	12.25±2.5	20 m	3	0.64±0.03	6.73±1.5
20 m	3	1.21±0.4	14.13±3.4	40 m	2	0.61±0.09	4.72±0.6
40 m	3	0.99±0.12	10.34±1.4				
Acropora palmata				*Agaricia lamarcki*			
5 m	2	3.32±0.13	18.8 ±2.3	40 m	2	3.49±0.6	8.95±1.9
Acropora cervicornis				*Agaricia undata*			
15 m	2	3.96±0.07	7.9 ±0.31	66 m	1	1.26	5.53
				Agaricia grahamae			
				80 m	3	1.52±1.2	3.2 ±0.7

Variations with shape

One of the most easily quantified measures of growth form is the surface area to volume (S/V) ratio, and Porter (1976) has used this ratio to demonstrate a correlation between polyp size, degree of heterotrophy, and growth form. From Figure 1 it is clear that at any depth considered, the branching forms (*Acropora palmata* and *A. cervicornis*) and plate-like forms (*Agaricia lamarcki*) have higher rates of respiration per unit weight of tissue than the massive *Montastrea* species.

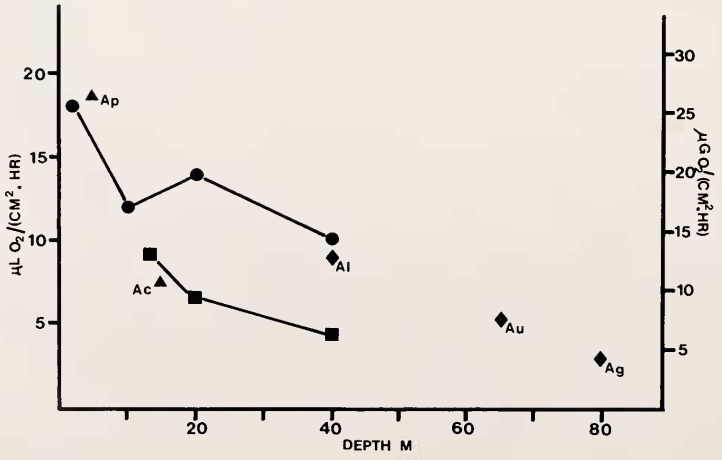

FIGURE 2. Surface-area-related respiration rate of corals plotted against the depth at which they were living. Symbols as in Figure 1

When the respiration rate is plotted against the S/V ratio for each coral (from Davies, unpublished) an almost linear relationship emerges (Fig. 3).

Discussion

Most previous workers who have measured the rates of respiration of corals have used the values obtained to compare oxygen production in the light to respiration in darkness (*e.g.* Yonge *et al.*, 1932; Kanwisher and Wainwright, 1967; Roffman, 1968), in which case a unit-weight or surface-area basis of comparison is not necessary. Kawaguti (1937) and Pillai and Nair (1972) did express results on a unit-weight basis but used the weight of the whole colony. This has the disadvantage of underestimating the rate of respiration by the living tissue, particularly in massive corals where the weight of skeleton may be 30 times that of the tissue. Recently McCloskey, Wethey and Porter (1978) have drawn attention to the need to adopt a standard unit for expressing both respiration and photosynthesis by corals, and have recommended the use of the unit of grams nitrogen of coral tissue. In the present study, results have been expressed in terms of both surface area and dry weight of coral tissue. Except in highly branched corals, surface area is simple to measure; and in studies on productivity, where knowledge of the area available to gather incident light is of prime importance, this method is probably preferable. However, the biomass of tissue per unit of surface area varies among coral species. Thus in Figure 2 it would appear that *Acropora palmata* has a higher rate of respiration than *A. cervicornis*. However, *A. palmata* has a very much greater weight of respiratory tissue per unit surface area than *A. cervicornis* (Davies, unpublished). When compared on a unit-weight basis (Fig. 1) it is apparent that *A. cervicornis* has the higher rate of respiration. For investigation of energy budgeting in corals or for comparison of energy expenditure under different conditions, unit-weight-related oxygen-consumption measurements are to be preferred.

In both *M. annularis* and *M. cavernosa* there is a decrease in weight-specific respiration rates with increase in water depth. The same observation is apparent when making interspecific comparisons between *Agaricia lamarcki* and the deeper

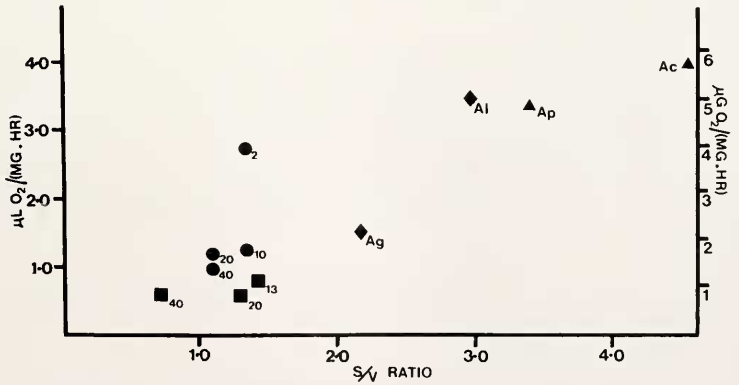

Figure 3. Weight-specific respiration rate of corals plotted against surface area to volume (S/V) ratio. Solid triangle, *Acropora*—Ap *Acropora palmata;* Ac *Acropora cervicornia;* solid diamond, *Agaricia*—Al *Agaricia lamarcki;* Ag *Agaricia grahamae;* solid circle, *Montastrea annularis;* solid square, *Montastrea cavernosa.* The depths (m) at which the *Montastrea* specimens were living is indicated.

water *A. undata* and *A. grahamae*. Since a proportion of the oxygen consumption can be attributed to the zooxanthellae, which may have different rates of respiration per unit weight than the coral tissue, the depth-related differences in respiration rates of the colonies might be explained by changes in the numbers of zooxanthellae in the tissues. However, Drew (1972) demonstrated in a series of Indo-Pacific corals that there was almost no change in the numbers of zooxanthellae per cm^2 of coral tissue with increasing depth, and preliminary experiments carried out in the present study confirmed this.

It is likely, therefore, that the respiration differences represent true differences in energy expenditure. If it can be assumed that the energy requirements for maintenance (i.e. for steady-state active transport and biosynthesis) of a unit weight of tissue would be the same in a shallow-water as in a deep-water coral, then the difference could be accounted for by the energy expenditure in biosynthesis for growth. Evidence for decrease in growth rate with depth in *Meandrina meandrites* has been obtained by Bak (1976) who measured skeletal weight underwater, and by Barnes and Taylor (1973), who demonstrated that the rate of uptake of ^{45}Ca was 55% higher in the central corallites of shallow-water (9 m) specimens of *Montastrea annularis* when compared with those living at 33 m. However, it should be borne in mind that in the present series of experiments the rate of respiration was measured in darkness, when skeletogenesis would be at a diminished rate (Pearse and Muscatine, 1971; Chalker and Taylor, 1975). Nevertheless, it is possible that for the duration of the experiments tissue growth was continuing. On the assumption that corals with a high rate of skeletal growth have a correspondingly high rate of tissue growth, it is likely, therefore, that we are here observing depth-related differences in energy consumption for the growth of new tissues.

A hitherto unsuspected correlation of respiration rate with growth form is suggested by Figure 3. The higher the S/V ratio, the higher is the rate of respiration per unit weight of tissue. Again, it is probable that this can be explained on the basis of differences in growth rates, since Bak (1976) has shown that the growth rate, or increment of new skeleton added per unit time, is higher by a factor of about 10 in high S/V forms (*Acropora palmata, Agaricia agaricites*) when compared with corals, such as *Montastrea annularis* and *Meandrina meandrites*, which have a low S/V ratio.

The actual rate of growth of any coral will be determined by both intrinsic factors, such as growth form, and by environmental factors, which include the level of nutritional intake. Porter (1976) has argued from morphometric grounds that high S/V corals, with small polyps, are adapted to a metabolic economy based largely upon the nutritional input of carbon compounds synthesised by the zooxanthellae. Their high respiration rates and growth rates are indications of the success of this.

In comparing deep-water and shallow-water corals of the same growth form, the lower respiration rates and growth rates of the former may be attributable to a low level of nutritional input.

It has been shown (Davies, 1977) that the quantity of carbon fixed by zooxanthellae in deep-water specimens of *Montastrea* may be only 20–25% that of shallow water specimens. If the intake of zooplankton is similar at the two depths, then the total nutritional input will be lower in the deep-living corals. In this way, respiration rate and growth rate would be determined primarily by the

change in input of carbon compounds by the zooxanthellae with change in light intensity accompanying change in depth.

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Summary

1. The rate of oxygen consumption of a number of Caribbean corals was determined, in darkness, and the results expressed on a unit-weight and unit-surface-area basis to enable inter- and intraspecific comparisons to be made.

2. Intraspecific comparisons of *Montastrea annularis* and *M. cavernosa* and comparisons between species of *Agaricia* show that corals living in deep water (40 m) have lower rates of respiration than shallow-water corals.

3. Corals, such as *Acropora* and *Agaricia*, with a high surface-to-volume ratio have higher rates of respiration per unit weight than the massive corals like *Montastrea*.

4. It is suggested that differences in rate of respiration are the result of differences in energy expenditure in the biosynthesis of tissue growth and that this is determined to a large extent by the nutritional input into the colony from the zooxanthellae.

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